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SOME FACTORS BEHIND DENSITY DYNAMICS OF BAT FLIES (DIPTERA, NYCTERIBIIDAE) — ECTOPARASITES OF THE BOREAL CHIROPTERANS: OMITTED PREDICTORS AND HURDLE MODEL IDENTIFICATION

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Some Factors Behind Density Dynamics of Bat Flies (Diptera, Nycteribiidae) — Ectoparasites of the Boreal Chiropterans: Omitted Predictors and Hurdle Model Identification. Orlova, M. V., Kshnyasev, I. A., Orlov, O. L. Zhigalin, A. V. — We investigated density dynamics of three bat flies species (Diptera, Nycteribiidae): *Penicillidia monoceros* Speiser, 1900, *Nycteribia quasiocellata* (Theodor, 1966), *Basilia rybini* (Hurka, 1969) parasitized on two host species: pond bat, *Myotis dasycneme* (Boie, 1825), and eastern water bat, *Myotis petax* Hollister, 1912. Females of *M. dasycneme* have 3.4 (95 % CI 1.4–8.3) times higher odds of being infested, and in 2.4 (1.5–3.7) times higher average number of *P. monoceros* than males. Similarly, females of *M. petax* have 1.7 (1.2–2.4) times higher density of *N. quasiocellata* and/or *B. rybini*. We hypothesized an existence of host-sex-recognition mechanism in bat flies, providing it fine "ecological profit" due to sex-biased dispersal among adult host during wintering and the chance to infested a host offspring later (in summer). The decrease (due to mortality or emigration) in density of bat flies can be described as simple harmonic or S-shaped curve, and its "step" apparently corresponds to time of host pairing.

Key words: ectoparasites, super-infestation, bat flies, Nycteribiidae, *Nycteribia quasiocellata*, *Basilia rybini*, *Penicillidia monoceros*, count regression, model identification, omitted predictors

Факторы динамики численности кровососущих мух — эктопаразитов рукокрылых (Diptera, Nycteribiidae): барьерная роль и неизмеримые предикторы. Орлова М. В., Кшнясев И. А., Орлов О. Л., Жигалин А. В. — Исследована сезонная динамика плотности трех видов кровососущих мух (Diptera, Nycteribiidae): *Penicillidia monoceros* (Speiser, 1900), *Nycteribia quasiocellata* (Theodor, 1966), *Basilia rybini* (Hurka, 1969) — эктопаразитов двух видов-хозяев: прудовой ночницы — *Myotis dasycneme* (Boie, 1825) и восточной ночницы, *Myotis petax* Hollister, 1912. Показано, что самки *M. dasycneme* характеризуются как в 3,4 (95 % ДИ 1,4–8,3) раза более высокими шансами инвазии, так и в 2,4 (1,5–3,7) раза более высокой средней численностью *P. monoceros*, чем самцы. Аналогично и самки *M. petax* имеют в 1,7 (1,2–2,4) раза более высокую плотность двух других видов кровососок *N. quasiocellata* и/или *B. rybini*. Мы предположили существование у мух-кровососок механизма распознавания пола хозяина, обеспечивающего сумму адаптаций эктопаразита дополнительным «бонусом» в форме анизотропной (с самцов на самок) миграции во время спаривания и зимовки рукокрылых, а в летнее время и возможностью заселения ювенильных особей. Сезонная динамика численности кровососок может быть описана простой гармонической функцией с периодом 1 год или S-образной кривой (при специальном выборе «начала отсчета»), «ступенька» которой сопоставляется по времени с периодом спаривания рукокрылых.

Ключевые слова: эктопаразиты, суперинвазированность, кровососущие мухи рукокрылых, Nycteribiidae, *Nycteribia quasiocellata*, *Basilia rybini*, *Penicillidia monoceros*, счетная регрессия, спецификация моделей, неизмеримые предикторы.

Introduction

The ecology of bat ectoparasites is rather interesting because of poorly studied, which is partly caused by the restricted hosts' availability for investigation during the winter, which lasts up to six months in Northern Eurasia (Bol'shakov et al., 2005). Poor or conflicting data on the bat ectoparasites ecology is contrasted with relatively well studied host biology (Strelkov, 1970; Bol'shakov et al., 2005) and doesn't allow forming holistic knowledge of the life cycle of this extremely specialised group of parasites.

The lack of ectoparasite reproduction during host hibernation is explained by some researchers (Lourenco, Palmeirim, 2008) by the low temperature in bats' winter shelters (caves in Southern Europe) that can be easily interpreted as an example of a strong decrease of reproduction capacity in insects and arachnids at temperatures below +8–10°C. However, the reproduction of gamasid mites during host hibernation was described by Dusbabek (1972) in Central Europe. Since the observations in Europe were done on bats wintering in caves at temperatures above +8 °C (10–12 °C), simple extrapolation of these results to the Russian temperate zone, where temperatures in bat winter shelters does not exceed +5 °C (usually +3–4 °C) may be invalid. Moreover, even own data from Urals and Western Siberia is ambiguous. Therefore, as the gamasid mites in reproductive condition and larvae in adult transformation were not observed in the winter at the North and Middle Urals (Orlova et al., 2012), mite females with intrauterine eggs, larvae, and deutonymphs (short, not feeding stages) were collected in Western Siberia (Barsukovskaya cave). The last observation indicates that the maturation of ectoparasites throughout host wintering may occur in the studied caves, despite a similar low temperature (+4 °C). Therefore, the consideration that temperature is the only factor that determines the reproduction of ectoparasites in winter seems premature.

Ectoparasites preferences of host species and host sex are also poorly studied. European authors noted a higher infestation on females and young in summer shelters (Christe et al., 2000; Lourenco, Palmeirim, 2008). Despite these observations being made during bat breeding season only, we found that this pattern is also obviously true for wintering colonies (Orlova et al., 2012). It is difficult to draw a more definite conclusion, because the research was conducted on a limited number of bat individuals.

According to the degree of dependence on its host species, the bat flies are considered to be permanent or temporary ectoparasites with long feeding, constantly living on the host body surface (or in its wool) and only leave it to hatch larvae (Balashov, 2009). Once deposited, the larva (sometimes referred as a prepupa) immediately forms a puparium. After a pupal stage that lasts three to four weeks, a new generation of adult flies emerges and must locate and colonize its host. Direct prepupa deposition on the host's body has been reported, but the pupae were distorted in shape and most of them failed to develop into adult flies. Usually males mate with females (sometimes of the new generation) immediately. Single mating is needed to produce some generations of offspring because females are able to store sperm. Pupae are deposited with about nine day interval. Nycteribiid flies are unable to live longer than a day outside of *their host's* body (Dick, Patterson, 2006). The existence of several separated faunistic complexes (European-Urals, Siberian-Far Eastern and transpalaearctic) is a feature of bats and bat ectoparasite fauna in the boreal Eurasia (Orlova, 2014; Orlova, Orlov, 2015), and so we focused our study on similarities and peculiarities of demography in bat flies belonging to separate faunistic complexes through host wintering.

Material and methods

Studied species and study area

We selected the most common bat flies, *Penicillidia monoceros* Speiser, 1900, *Nycteribia quasiocellata* (Theodor, 1966), and *Basilia rybini* (Hurka, 1969), as the subject of our study. Data collection (fig. 1) was carried out for: 1) *P. monoceros* — in Smolinskaya cave (Sverdlovsk Region, Middle Urals, 56°28′ N, 61°37′ E) throughout bat wintering in 2010–2011, from mid-October to mid-April, nine tours with about one month intervals; 2) *N. quasiocellata* and *B. rybini* — in Barsukovskaya cave (Novosibirsk Region, Western Siberia, 54°22′ N, 83°58′ E), third tours — from November to the end of March in 2013–2014. We included the results of the bat flies census in the summer shelters (July 2007), collected in the Khanty-Mansiysk Autonomous Region (Korliki village, Nord-West Siberia, 61°32′ N, 82°25′ E). Since any agitation for hibernating bats is extremely undesirable, and the pond bat *Myotis dasycneme* (Boie, 1825) is a protected species, we examined only a limited number of individuals (84 *M. dasycneme* and 51 eastern water bats *Myotis petax* Hollister, 1912). Unfortunately, age determination methods for unlabelled bats have not been developed yet, so this effect on infestation risk and mean flies abundance will not evaluated explicitly. Altogether we collected 107 specimens of *P. monoceros* from *Myotis dasycneme* (Boie, 1825), 234 specimens of *N. quasiocellata* and specimens of 196 *B. rybini* from *Myotis petax* Hollister, 1912.

Statistical analysis

A standard statistical tool for count data (positive integers) modeling is (usually via log-link) Poisson regression (special case of GLM — generalised linear models) (McCullagh, Nelder, 1989). However, in reality, quite often the census data are characterized by strong deviations from the theoretical Poisson distribution that describes a simple and purely stochastic process and has a single (mean-variance) parameter λ: $E(Y_i|x_i) = \mu_i$, μ_i ~

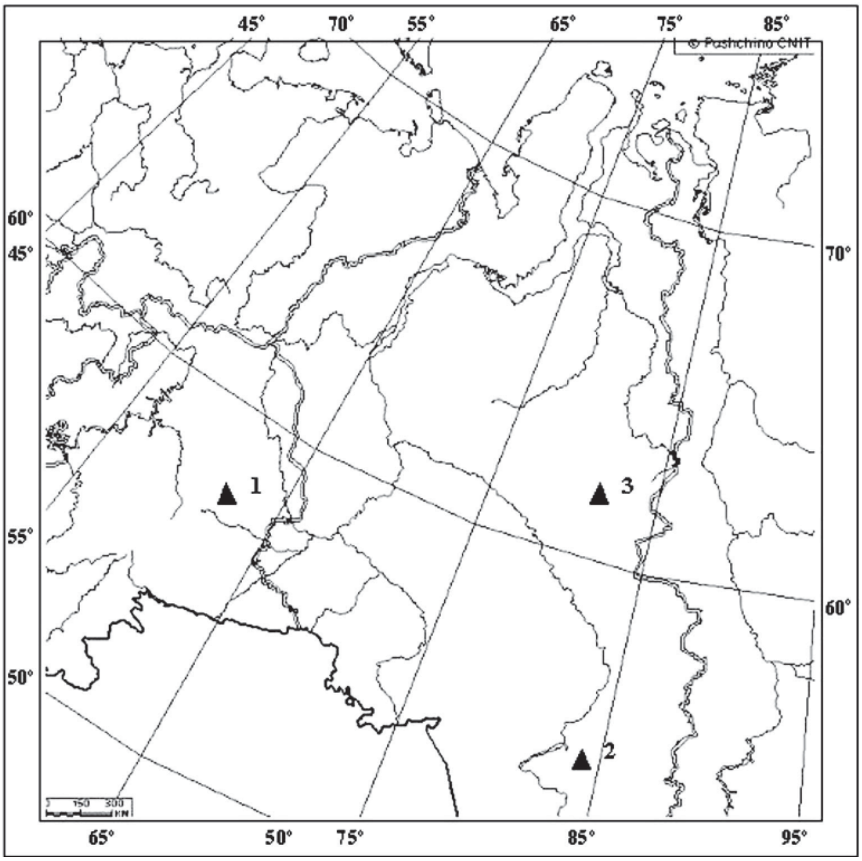


Fig. 1. Study area: winter bats colony — Smolinskaya (1) and Barsukovskaya (2) caves, Korliki village — summer settlement (3).

Poisson (λ_i), $\lambda_i > 0$. For example, an excess (relative to the standard Poisson distribution) of zero values (ZIP — Zero Inflated Poisson) and/or violations of assumptions about the parameter variance Var (μ_i) ≠ μ_i.

The unconditional distribution of being categorized by the host sex and census time "raw data" is not surprising — the observed number of bat flies, wither free from flies individuals or after the truncation of the zeros (fig. 2) does not fit to the Poisson distribution (Kolmogorov–Smirnov test, d = 1.65, p < 0.01). There is not only an excess of zeros (many hosts were free from ectoparasites) but also an excess of animals infested of single bat fly too as well as "heavy right tail" — "super-infested" individuals with unexpectedly high ectoparasite counts. For the statistical modelling of such heterogeneous count data we used the hurdle model, involving a combination of several data generation processes (Mullahy, 1986; Cameron, Trivedi, 1998; McDowell, 2003; Stavishenko, Kshnyasev, 2013). Previously, we found (based on Vuong test statistic = –6.61 and –11.98, which is asymptotically distributed as Normal (0.1) under the null hypothesis that the models are indistinguishable) and that hurdle models were superior to standard Poisson or Negative Binomial regressions models for our data (detailed result not shown here). This kind of parameterization, furthermore, ensures that there is no possible (though unlikely) bias via the repeated sampling of a previously "purified" host (note, we used unlabelled bats, but not fewer than 2 individuals were caught twice because it has the sign of previous tissue sampling for molecular genetic analysis on its wing membrane). The hurdle model is specified as a combination of two regression equations:

$$\eta = \text{logit}\,(Y) = \beta X,\ Y = 0 \text{ or } Y = 1 \text{ if } Y_i \geq 1 \ (1)$$

$$g = \log\,(Y) = \beta X,\ Y_i \geq 1 \ (2).$$

As the binary part of our hurdle model the logit regression (Eq. 1) was used to estimation the probability of host infestation (not displayed in the table, see text). The expected bat flies number on infected bats we modeled via quasi-Poisson regression (Eq. 2), controlling for equidispersion ($\phi = X^2/df \approx 1$). For model comparisons for the count part of the hurdle model we used AIC — Akaike information criterion (without any ϕ — correction here, but see Anderson et al., 1994): AIC = –2logL+2K, where the first term is the deviance and the second — penalty for model complexity. We obtained Maximum Likelihood estimates for the b_j — log-effects of the following predictors (X_i): time since a fixed date (15 July) or just parts of bats wintering (before/

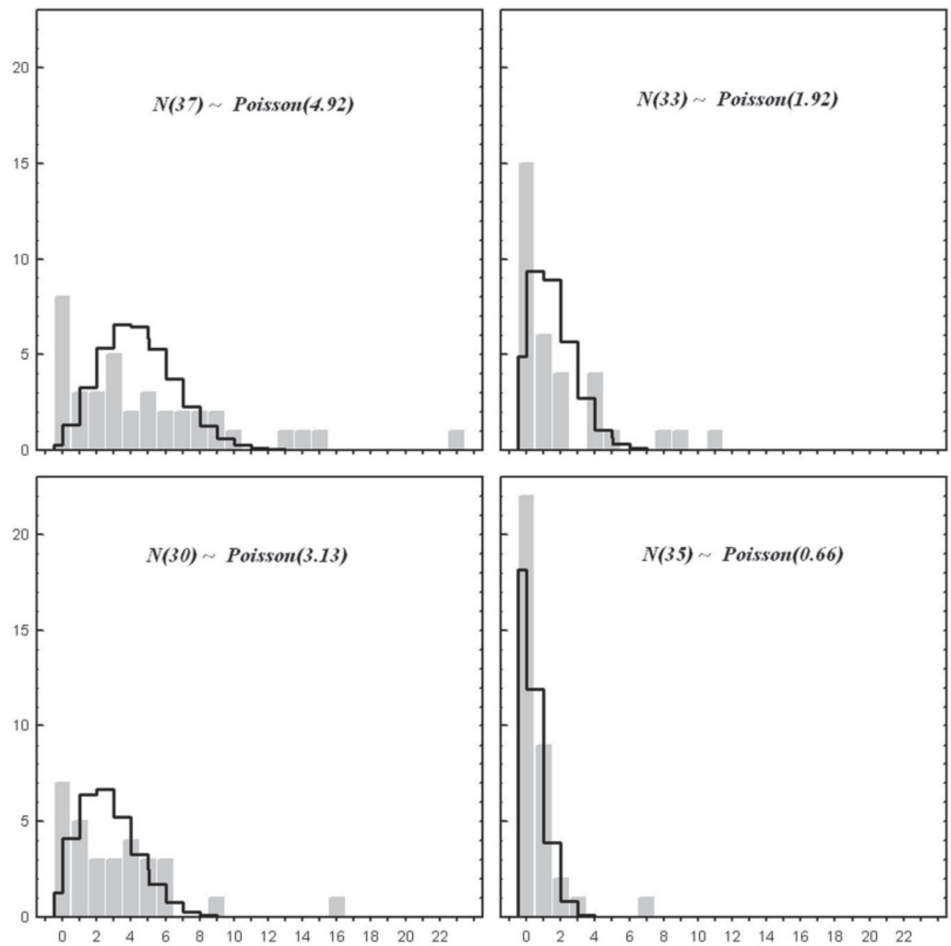


Fig. 2. Observed (bars) and expected (PMF) host infestation by Nycteribiidae bat flies: before/after (top/bottom) host mating; host females/males (left/right). *No zero truncation and the used categorisation (pooled both host species and bat flies species) are the reasons of relatively bad fit to Poisson distribution.*

after host mating); the logarithm of the number of bat flies species can be used as an offset variable (only the eastern bat is characterized by two species of bat-flies), or can be explicitly modeled (as we have done), and the exponentiation of this coefficient gave the rate ratio for the average infestation of two studied bat species or for two bat faunal assemblages. Unfortunately, as immeasurable age of the host could not been modeled explicitly (omitted predictor), we added "ad hoc" its surrogate (presumably replacing the latent host age) dummy predictor, that marked apparently "super-infested" individuals, a conditional dichotomizing threshold was adjusted iteratively — until a satisfactory fitting both predicted to observed values and the dispersion parameter to assumption of Poisson process ($\phi \approx 1$). Quasi-Wald statistic and 95 % confidence intervals for quasi-Poisson regression coefficients were calculated taking into account the estimated dispersion inflation factor: $b_i \pm 1.96\phi^{0.5}SE\ (b_i)$, the last is given in the text (or table) after exponentiation, $\exp\ (b_i)$ or $(\exp\ (b_i))^{-1}$, and can be easy interpreted as a rate ratio (or odds ratio in binomial part, respectively) — the change in response by unit predictor change (table 1). Because there is no evidence for winter reproduction of bat flies in the study area, the interpretation of regression coefficients at a predictor "time" (or part of winter) is greatly simplified and can be assigned to bat flies mortality and dispersion.

Results and discussion

All species of bat flies in Russia belong to the family Nycteribiidae. The Nycteribiidae flies are highly specialised ectoparasites, in which most of them are monophagous or oligophagous parasites of several species of one genus and are rarely of different genera (Dick, Patterson, 2006). *Penicillidia monoceros* considered to be density-dependent oligopha-

T a b l e 1 . Model selection and parameter estimations of quasi-Poisson regression for the count part of the hurdle model for bat fly density on its host

Predictors	b	se $\times\phi^{0.5}$	Q-Wald	P ≤	Exp (b)*	–95 %CI	+95 %CI
			No 1: k = 5, ΔAIC = 0; w = 0.531				
Interc#	1.05	0.08	173.75	0.001	2.85	2.50	3.25
sexHost	–0.47	0.11	18.59	0.001	1.61	1.34	1.93
Extr[a]	1.38	0.17	69.79	0.001	3.98	3.03	5.22
Out[b]	1.07	0.10	107.00	0.001	2.92	2.46	3.46
log (nspec)**	0.78	0.14	29.50	0.001	2.19	1.73	2.77
Scale, $\phi^{0.5}$	0.87						
			No 2: k = 6, ΔAIC = 0.25; w = 0.468;				
Interc	1.13	0.09	150.55	0.001	3.09	2.66	3.59
sexHost	–0.47	0.11	19.54	0.001	1.60	1.34	1.91
PartWint[c]	–0.16	0.10	2.42	0.120	1.17	0.99	1.38
extr	1.41	0.16	76.75	0.001	4.09	3.14	5.32
Out	1.03	0.10	100.31	0.001	2.80	2.37	3.32
log (nspec)	0.74	0.14	26.79	0.001	2.09	1.65	2.64
Scale, $\phi^{0.5}$	0.84						
			No 13: k = 5, ΔAIC = 63.46; w = 9E-15				
Interc	1.38	0.14	102.22	0.001	3.96	3.03	5.17
sexHost	–0.40	0.17	5.96	0.015	1.50	1.08	2.07
PartWint	–0.34	0.15	5.31	0.021	1.41	1.05	1.89
extr	1.10	0.23	22.18	0.001	2.99	1.90	4.72
log (nspec)	0.95	0.22	18.93	0.001	2.58	1.68	3.95
Scale, $\phi^{0.5}$	1.28						
			No 19: k = 4, ΔAIC = 90.69; w = 1E-20				
Interc	1.37	0.15	80.67	0.001	3.92	2.91	5.28
sexHost	–0.47	0.18	6.56	0.010	1.59	1.12	2.27
PartWint	–0.27	0.17	2.71	0.10	1.32	0.95	1.82
log (nspec)	1.15	0.23	24.68	0.001	3.17	2.01	4.99
Scale, $\phi^{0.5}$	1.43						

S y m b o l s : # — the constant term is interpreted as (log) expected bat fly density in the "normally" infested pond bat females (before mating, if a model contains last predictor); *— Rate Ratio = exp (b) or 1/exp (b) — see the sign of b-coefficient; ** — the effect of host bat species (eastern bat) and/or place (Western Siberia), it can be used as offset, but here we introduced it explicitly as an independent variable for the sake of compare it with a prior expected value = 2; a — indicator variables for two extreme numbers (23, 16) of bat fly; b — possible outliers (note, the a & b can be used as single marker, but here it was convenient to show that its coefficients looks similar — see CI); c — second part of wintering, after host mating.

gous ectoparasite concatenated with pond bats, at least in areas with a high abundance of *Myotis dasycneme* (Leningrad Region, Urals), but it becomes oligophagous on the genus *Myotis* in the rest of Northern Eurasia (Orlova et al., 2014 a). The pond bat belongs to the transpalaearctic chiropteral faunistic complex and presumably penetrated Western Siberia from the Europe throw Urals, and obviously the *P. monoceros* spreads eastwards with its host, since *M. dasycneme* is the only *Myotis* species that has overcome the "chiropterological desert" (part of Western Siberia territory where *bats* were in very *low numbers*) that separates European-Urals and Siberian-Far Eastern faunistic complexes (Orlova, 2014). *P. monoceros* is the most common bat fly in the Urals, and up to 70 % of pond bats were infested in the investigated winter colonies, with an average infestation rate of about three flies per host.

Nycteribia quasiocellata and *Basilia rybini* are (presumably) specific ectoparasites of *Myotis petax* or perhaps of other species within the genus *Myotis* in Siberia and the Far East

of Russia. Both species of flies are common in the Asian part of Russia, eastern Kazakhstan, and Mongolia (Orlova et al., 2014 b). We did not find any evidence of negative interspecies interference in the pair of *N. quasiocellata* and *B. rybini*, and odds of two/zero species infestation (27/4) in *Myotis petax* is 6.75 (MacNemar $X^2(1) = 5.61$), thus, we proposed the independence in nycteribiids demography (Fisher exact test for 2 ×2 table p = 1.0).

The decrease of the mean bat flies density on infested host during winter (ignoring other predictors) with nearly equal (but moderate) success can be described via a simple harmonic function (with a fixed period of one year and range (doubled amplitude) = 3.0, $R^2 = 0.12$) or (with specially selected start time) monotonous exponential decay ($R^2 = 0.11$) or S-shaped function ($R^2 = 0.12$, F (3; 80) = 39.22) (fig. 3). The similar pattern was observed previously for gamasid mites *Macronyssus corethroproctus* (Orlova et al., 2012). A timing of the maximum rate of decrease in the mean infestation separates two parts of host wintering and can be associated with the mating period in *Myotis* bats (op. cit.). Note that the host mating gives ectoparasites a unique chance to migrate (change a host), but it may not always be successful because of host grooming.

If we do not "forcibly" introduce the "super-infestation" as an additional predictor in the model equation and proposed parallelism in the rate of decrease, the estimated infestation rate ratio (from the first to second part of wintering) in two *Myotis* species under investigation is 1.5 (95 % CI 1.04–2.0) (fig. 3). It should be noted, however, that the decline in the mean infestation is not only due to mortality in ectoparasites, but also anisotropic (mainly from host males to females) migration. The possibility of such migration is supported by our direct observation, so one of the two recaptured "tagged" and previously fully deparasitized females, already carried 4 ectoparasites at the time of repeated observations; the second female remained free from bat flies. Lastly, this suggests that higher bat fly numbers on a host female as described by European authors and explained only

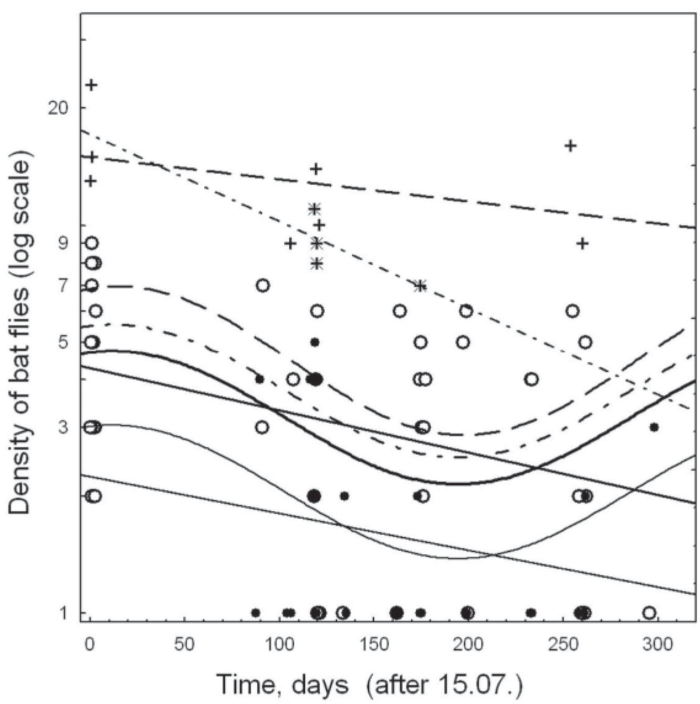


Fig. 3. Observed (all kinds of dots) and expected (lines: y = exp (m+Acos (2pi (x–c)/36 — f) or $y = b_0 exp(-b_1 x)$) seasonal density dynamics of Nycteribiidae bat flies. Filled circles and thin lines — normally infested males; open circles and solid lines — normally infested females; double crosses and dashed lines — super-infested males; crosses and dashed lines — super-infested females. N o t e : Infested host only.

as a result of higher ectoparasite reproductive output, is rather the consequence of their initially higher infestation (at the time of host migration from winter shelters). Since bat females share summer shelters, it gives bat flies another chance to infest other hosts and the young of the year.

The predicted infestation for the *Myotis dasycneme* female (from Urals) at the beginning of winter is approx. 3.9 (95 % CI 2.9–5.3) nycteribiids. *Myotis petax* (carried two bat fly species) is characterized by a 3.2 (95 % CI 2.0–5.0) times higher fly density. The sex bias in bats infestation shows clear and similar patterns in both faunal assemblages, and *Myotis* males on average has fewer flies by 1.6 (95 % CI 1.1–2.3) times. The last estimation is consistent with the assumption of the existence of a sex recognition mechanism in ectoparasites, providing to the last a some profit as a possibility to parasitise on the young of the year later, when the females leave its winter shelters (caves) and form brood colonies in the summer shelters (hollows, lofts, etc.), while males may remain in winter shelters.

As in the case of a parasitic gamasid mite, *M. corethroproctus* (Orlova et al., 2012), the so-called "super-infested" bats exist in our new data, which are characterised by a 3.5 times higher number of bat flies, and such animals were found either among pond bats or eastern water bats. The extremely high infestation of individuals can be explained by their low immune status, or some unexplored characteristics (age, etc.). For example, we can speculate in next manner: as an individual is older (especially female), then it came through more matings (that giving a chance for ectoparasite for migration) and summer ectoparasite reproduction cycles and the risks of infestation and a mean number of ectoparasites are increased correspondingly.

For host females (unconditionally of host species and observation time) the risk (52/67 or 0.78) of being infested of Nycteribiidae bat flies is estimated in 1.7 (95 % CI: 1.3–2.3) times higher ($Z = 3.6$, $p = 0.0003$) than for males (31/68 or 0.46).

The estimated (unconditionally of the observation time, sex, etc.) average risk (36/84 or 0.43) for *M. dasycneme* (which parasitized only Nycteribiidae species) is in 2.15 (95 % CI: 1.66–2.79) times lower ($Z = 5.78$, $p \leq 0.0001$) than for *M. petax* (47/51 or 0.92). The last is in perfect agreement with a prior expectation of its twofold increase if the host has two bat fly species. This is consistent with our observation of higher infestation by other ectoparasites in *M. petax* (Orlova et al., 2014 b).

Thus, three Nycteribiidae species are characterised by a similar population dynamics during the winter and host hibernation (the decreasing in average number with a steep descent, probably timing the host mating), despite these bat flies parasitizing hosts belonging to two separate complexes of bat fauna. We find a strong preference of host females by ectoparasites, and hypothesised a possible redistribution of ectoparasites through host mating, when bat flies move from the host male to female mainly.

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